THE CROCODILIAN *BERNISSARTIA* IN THE WEALDEN OF THE ISLE OF WIGHT

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ABSTRACT. Isolated rounded teeth from the Wealden of the Isle of Wight are shown to belong to the small crocodilian *Bernissartia*, hitherto known only from the Wealden of Belgium. A partial skeleton from the Wealden of Hastings, described by Owen as '*Crocodilus saulii*', is also referred to this genus. Similar rounded teeth have also been found in the Wealden of eastern Spain, and possibly in the Lower Cretaceous Trinity Formation of Texas. The crushing posterior teeth of *Bernissartia* are probably indicative of a specialized diet including a large proportion of hard-shelled molluscs.

WHILE searching for mammal teeth in the Wealden of the Isle of Wight, one of us (R. L. E. F.) observed the end of a large, flattened, lignified tree-trunk in the cliff-face. It appeared that this trunk must have lain in water, possibly a river, and that current action had scoured a hollow underneath it. As it seemed likely that heavier objects might have collected in the hollow, the sediment from under the tree-trunk was removed and sifted. It yielded several thousand teeth, including three mammal teeth, teeth belonging to several species of shark, many bony-fish teeth (mostly those of *Lepidotes*), teeth belonging to several species of dinosaur (including a megalosaur and *Hypsilophodon*), teeth of the large crocodilian *Goniopholis crassidens*, and a number of teeth of peculiar, button-like shape.

These specimens come from the south-west coast of the Isle of Wight, about midway between Compton Grange Chine and Hanover Point (map reference SZ 377840), at beach level in the second of the three lignitic bands depicted by Osborne White (1921, fig. 1, p. 12). Following this, samples were taken from the *Unio* bed on the cliff at Sudmore Point, about one mile further east. The clay from amongst the *Unio* yielded more of the button-like teeth, and a small number were also found in the Wealden Shales overlying the *Hypsilophodon* Bed at Cowleaze Chine, another four miles eastwards. In all these sites the teeth were found in freshwater deposits.

A total of about 40 of the button-like teeth were found and these were eventually identified (by E. B.) as belonging to the small crocodilian *Bernissartia* Dollo, which had previously been found only in the famous Wealden locality of Bernissart in Belgium.

DESCRIPTION

The teeth under discussion are represented only by crowns, the root having disappeared in all specimens. This may be due partly to the normal process of resorption of the root during tooth replacement, but differential preservation of the more resistant enamel-covered crown during fossilization is undoubtedly an important

[Palaeontology, Vol. 22, Part 4, 1979, pp. 905–912, pl. 122.]

factor. The centre of the base of the crown is bulging and surrounded by a slight concavity (Pl. 122, fig. 26); it thus appears that the pulp cavity did not prolong itself inside the crown. The latter was apparently sharply demarcated from the root.

The most obvious character of these tooth crowns is their low, blunt, rounded profile. There is a certain amount of variation in this respect; some specimens still show an obtuse but somewhat pointed apex and thus resemble the posterior teeth of many crocodiles; others, which presumably come from more posterior parts of the jaws, have a completely rounded semicircular profile. Some of the larger teeth are hemispherical and in occlusal view their outline is regularly oval. Others are more elongated, or even much compressed laterally. Some are definitely kidney-shaped, with a fairly sharp constriction at mid-length (Pl. 122, figs. 1 to 25). All these teeth are quite small. The largest one (Muséum National d'Histoire Naturelle no. 1978-2a, Pl. 122, fig. 1) has a transverse diameter of 3·9 mm and an antero-posterior diameter of 5·7 mm. For a much smaller, laterally compressed tooth (M.N.H.N. no. 1978-2b), the corresponding measurements are 0·8 and 2 mm respectively. The enamel of these teeth shows a distinct ornamentation. On unworn crowns, a longitudinal ridge or carina can be seen. From this ridge, fine wrinkles radiate on the sides of the crown. Nearer the base, however, the enamel becomes smooth, with only faint growth rings. As the tooth wore down, the enamel along the longitudinal ridge was soon destroyed, producing a shallow, narrow groove reaching into the underlying dentine. As wear proceeded, this groove was in turn replaced by a flat wear facet; in some instances, the apex of the crown is completely worn away and an extensive surface of dentine is exposed. Apparently, the teeth were not shed until they were much worn.

EXPLANATION OF PLATE 122

Figs. 1–20. Occlusal views of isolated teeth of *Bernissartia* sp. indet., from the Wealden of the SW. coast of the Isle of Wight between Compton Grange Chine and Hanover Point (collected by R. L. E. Ford), showing differences in size, shape, and degree of wear. Magnification: ×7. Specimens 2, 4, 6, and 8 are in the British Museum (Natural History), collective no. R 9296. The others are in the Muséum National d'Histoire Naturelle, Paris, collective no. 1978-2.

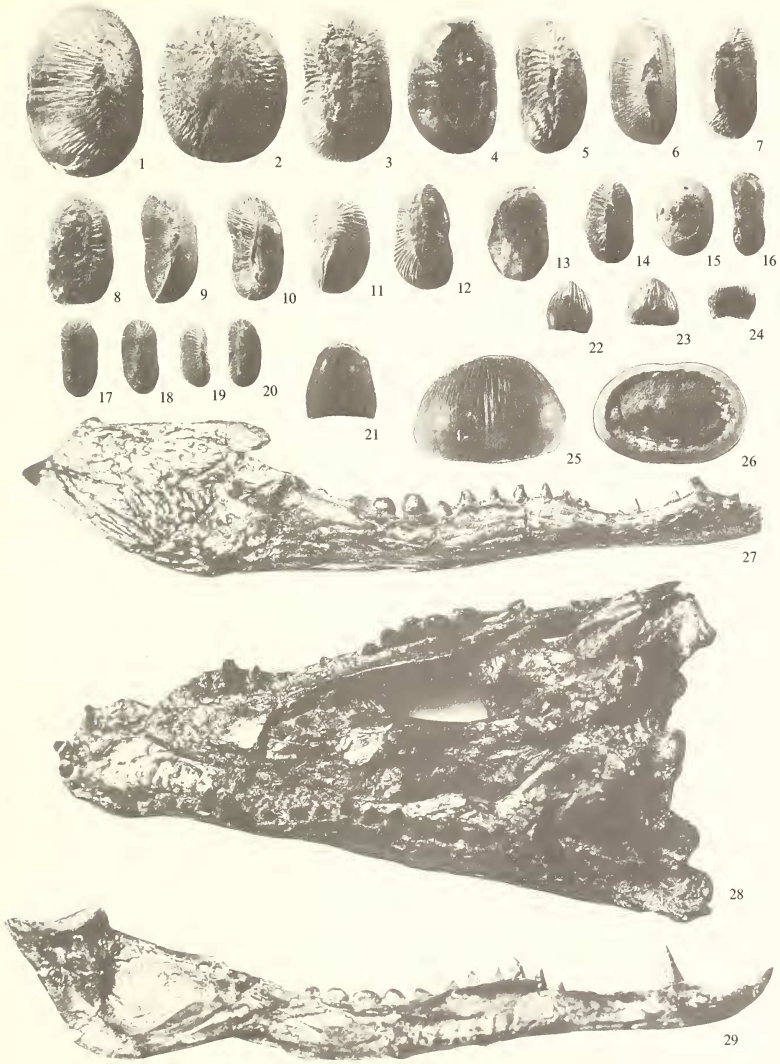
Figs. 21–24. Side views of four teeth of same origin, ×7. Fig. 24 is a posterior crushing tooth, while figs. 21, 22, and 23 are from more anterior parts of tooth rows. These four specimens are in the British Museum (Natural History), collective no. R 9297.

Fig. 25. Side view of the same tooth as fig. 1, showing the rounded outline of the crown and its ornamentation. Magnification: ×6.

Fig. 26. View of the base of the crown of the same tooth as fig. 25, showing the typical condition of this region on isolated crowns from tribodont crocodilians. Magnification: ×6.

Figs. 27, 28, 29. Lectotype of *Bernissartia fagesii* Dollo, from the Wealden of Bernissart (Belgium); Institut Royal des Sciences Naturelles de Belgique, Brussels, I.R.Sc.N.Br. no. 46. Natural size. Fig. 27: labial view of the right mandibular ramus, showing the posterior crushing teeth. Fig. 28: ventral view of the skull, showing the posterior crushing teeth. Fig. 29: lingual view of the left mandibular ramus, showing the association of pointed anterior teeth with crushing posterior teeth.

All photographs, except figs. 27, 28, and 29, by D. Serrette.



BUFFETAUT and FORD, Crocodilian *Bernissartia*

SYSTEMATIC POSITION

A dentition which comprises blunt, rounded teeth may be called 'tribodont' (Greek, τρίβω, to crush, and ὀδούς, tooth). Such teeth occur in several distinct groups of vertebrates (fishes such as *Lepidotes* and pycnodonts, lizards such as *Dracaena*, *Hemisphaeriodon*, some species of *Varanus*, the mosasaur *Globidens*, several species of ichthyosaurs, etc.), but the shape and ornamentation of the specimens from the Wealden of the Isle of Wight show the closest resemblances with those of the posterior teeth of some crocodilians, both living and fossil. The only really tribodont crocodile living today is the small and rather primitive crocodylid *Osteolaemus tetraspis* Cope, which is found in western and central Africa. In *O. tetraspis* the two most posterior teeth in each jaw are blunt, almost hemispherical; the tooth immediately anterior to them is of ogival shape. The best-known fossil tribodont crocodilians are a group of small alligatorids from the Palaeogene of North America and Europe. Most of them can be referred to the genus *Allognathosuchus* Mook, several species of which have been described, ranging from the Palaeocene to the early Oligocene (a list and short discussion of them is given in Berg 1966, and in Steel 1973). The number and relative size of the crushing teeth is somewhat variable according to the species. Alligatorids with a tribodont dentition are already present in the late Cretaceous, with the North American *Brachychampsa montana* Gilmore, from the Lance Formation of Montana (Gilmore 1911), and still-undescribed forms from southern France and Austria. Crushing posterior teeth seem to have been widespread in early alligatorids, since they also occur in the earliest known representative of the family, *Albertochampsa langstoni* Erickson, from the Oldman Formation of Alberta (Erickson 1972). Isolated teeth of *Brachychampsa* and *Allognathosuchus*, which are abundant in some North American and European localities, are virtually indistinguishable from the Wealden specimens discussed here, especially when the root has been destroyed.

However, a tribodont crocodilian is already known from the Wealden: *Bernissartia fagesii* Dollo, 1883, of which two skeletons (one of which is almost complete) were found in the famous locality of Bernissart (Belgium). Despite some progressive features, this small form (over-all length about one metre) apparently belongs to a mesosuchian family, the Bernissartidae (Dollo 1883, Buffetaut 1975). In *B. fagesii* the three most posterior teeth in both the maxilla and the dentary are low and completely blunt, and the two teeth just anterior to them are also rounded; Dollo (1883) coined for them the term 'pseudomolaires'. Further forward along the tooth rows, the crowns become progressively taller and more pointed (Pl. 122, figs. 27–29). The complete dentition of *B. fagesii* is known from the lectotype, kept in the Institut Royal des Sciences Naturelles de Belgique, Brussels (I.R.Sc.N.Br. no. 46).

As shown by direct comparison, the teeth from the Wealden of the Isle of Wight are identical to those of *B. fagesii*. Differences in shape observed in the series from England are explainable by tooth differentiation along the jaws: in *B. fagesii*, the lower crushing teeth are somewhat more compressed laterally than the upper ones, and some of them are kidney-shaped. Age differences may also have played a part, however, since examination of several specimens of *O. tetraspis* shows that in young individuals the crushing teeth are more compressed laterally than in older ones. Enamel ornamentation is also identical in our specimens and in *B. fagessi*, and so

is the peculiar apical wear pattern. The roots are visible on some of the lower teeth of the Brussels specimen: they are long, hollow, and flattened laterally; there is a sharp constriction at the limit between the root and the crown. It can easily be understood how the destruction of the root of such a tooth could lead to the peculiar appearance of the bases of the crowns from the Isle of Wight. The teeth of the anterior parts of the jaws of *B. fagesii* are conical, pointed, and slender, like ordinary crocodilian teeth. Teeth of that type have been found with the rounded ones in the Wealden of the Isle of Wight, and both may well belong to the same form, all the more so since there are specimens showing an intermediate shape. Lastly, the size of the teeth of the type of *B. fagesii*, which is probably an adult specimen, accords well with that of the larger specimens from the Isle of Wight.

Because of the above-mentioned resemblances, it seems safe to refer the rounded teeth from the Wealden of the Isle of Wight to the genus *Bernissartia*, sp. indet. On the basis of the available material, it would be premature to attempt a more accurate identification. The form from the Isle of Wight may well be conspecific with *B. fagesii*, but we need some skull material before this point can be settled.

GEOGRAPHICAL DISTRIBUTION OF THE GENUS *BERNISSARTIA*

As mentioned above, the genus *Bernissartia* was first described from the Wealden of Belgium, where it is known in a single locality, the coal-pit of Bernissart. Although the teeth described in this paper constitute its first well-attested occurrence in England, the presence of *Bernissartia* in this country has long been suspected. In 1851 Owen described and figured slabs of sandstone from Hastings containing remains of a small crocodile. This specimen, first thought to come from the Greensand, turned out to be Wealden in age (Woodward 1886). It consisted of various postcranial bones and the anterior part of the lower jaw. Owen subsequently (1884, index, p. vi) named it *Crocodilus saulii*. Woodward (1885) suggested affinities with *Bernissartia*, and Lydekker (1888, p. 77) wrote of the specimen that it is '. . . too imperfect to admit of generic identification, but it may be identical with *Bernissartia*'. Although the whereabouts of the jaw fragment seem to be unknown, the main slab is now (specimen no. R 37712) in the British Museum (Natural History); one of us (E. B.) recently had the opportunity to study it there. Careful scrutiny has revealed the presence of a small isolated tooth which is completely similar to those from the Isle of Wight described above, and to those of the Brussels specimen of *B. fagesii*. It is blunt, somewhat compressed, and its enamel is finely wrinkled. It thus seems safe to refer this fossil from Hastings to the genus *Bernissartia*, which is not inconsistent with the shape of the mandible as figured by Owen. A specific determination, however, is not possible on the basis of the available material.

There is also some evidence for the occurrence of *Bernissartia* outside north-western Europe. Crusafont-Pairo and Adrover (1966) and Berg and Crusafont-Pairo (1970) have reported isolated teeth reminiscent of those of *Allognathosuchus* from the Wealden of Galve, Province of Teruel, eastern Spain. Similar rounded teeth have also been collected in the same deposits by German workers (B. Krebs, pers. comm.). Although no figures are yet available, it seems very likely that these teeth actually belong to a bernissartid crocodilian, and possibly to the genus *Bernissartia*. This

would fit the age of the Galve locality much better than would *Allognathosuchus*, since the latter is known only from the Palaeogene. According to B. Krebs (pers. comm.), *Bernissartia*-like teeth have also been discovered in the Kimmeridgian locality of Guimarota, Portugal.

Lastly, the collection of fossil reptiles in the British Museum (Natural History) includes a few teeth from the Lower Albian Trinity Formation of Texas, presented by B. Slaughter. One of these, represented only by its crown, is bulbous, completely rounded, shows traces of apical wear, and much resembles *Bernissartia* teeth from England and Belgium. Although somewhat younger, the crocodilian fauna of the Trinity Formation, described by Langston (1974) and Thurmond (1974), is rather reminiscent of that of the Wealden of Europe, so the occurrence of a bernissartid in the Lower Cretaceous of North America would not be surprising (the North Atlantic Ocean was still unopened at this time). However, more material is needed before a definite conclusion can be reached.

THE FUNCTIONAL AND ETHOLOGICAL SIGNIFICANCE OF THE TRIBODONT DENTITION OF *BERNISSARTIA*

As pointed out above, blunt posterior teeth are known to occur in several groups of crocodilians. The problem of the functional significance of tribodont dentitions in crocodilians was first discussed at some length by Case (1925), who thought that *Allognathosuchus* had '. . . a durophagous, probably conchifragous diet'. Abel (1928) devoted a whole paper to that problem, and concluded that *Allognathosuchus* fed on turtles, whose shells could be crushed by its specialized teeth and jaws, but his reconstruction of the dentition of this form was erroneous, in that he assumed that even the anterior teeth were blunt and low-crowned. Simpson (1930) expressed a contrary opinion, considering that the dentition of *Allognathosuchus* was no evidence of a specialized diet, but rather suggested versatility. More recently, as a conclusion to his study of the early Oligocene tribodont alligatorid *Balanerodus loginus*, from Colombia, Langston (1965, p. 116) concluded: 'That *Balanerodus* and *Allognathosuchus* were durophagous by adaptation and preference seems a reasonable assumption to me.' As pointed out by Simpson (1930), in many crocodilians the posterior teeth are indeed blunter than the anterior ones. However, the condition in the tribodont forms mentioned above seems to depart sufficiently from the usual one in crocodiles to allow us to assume that they had a specialized diet, somewhat different from that of more 'classical' crocodiles. It is difficult to escape the conclusion that the food of tribodont crocodilians consisted largely of animals with a hard shell. The peculiar wear pattern of the posterior teeth seems to confirm this view since, in occlusion, as already pointed out by Berg (1966) in the case of *Allognathosuchus*, the upper and lower teeth of tribodont crocodilians do not come into contact as they do in mammals. In *Bernissartia fagesii*, tribodont alligatorids such as *Allognathosuchus*, and *Osteolaemus tetraspis*, the labial part of the lower teeth can come into contact with the lingual part of the upper ones, but this can hardly explain the broad and flat wear facets observed on the crowns. In all likelihood this strong wear was due to the crushing of hard foodstuffs. It is of course difficult to determine exactly what this food was in the case of fossil forms. Contrary to Abel's opinion (1928), some

recent crocodiles are now known to eat molluscs and crabs, and this is true of forms which do not exhibit a particularly specialized dentition. For instance, Cott (1961) writes of *Crocodylus niloticus* that 'one of the surprising facts here brought to light is the quite unexpected role of molluscs in crocodile ecology'. Unfortunately, the ecology of the only living tribodont crocodile, *O. tetraspis*, is still poorly known. According to Wermuth (1953), however, this species feeds on molluscs and crabs, which possess a hard shell. Kälin (1941) and Antunes (1962) also describe *O. tetraspis* as 'durophagous'.

Since mollusc-eating habits are apparently widespread in crocodilians, the evolution of a specialized crushing dentition in some forms probably conferred some selective advantage. In an environment such as that of the Wealden of north-western Europe, where a number of crocodilian species are known to have lived, a tribodont dentition may have allowed *Bernissartia* to exploit a particular food source more efficiently. Possible prey for this form in the Wealden of the Isle of Wight include the freshwater mussel *Unio valdensis*, the lamellibranch *Filosina gregaria*, and, among gastropods, two species of *Viviparus* (*V. elongatus* and *v. fluvianus*) and a small planorbid, *Anisopis* cf. *fisheri*. Turtles of course were also present but, because of its small size, *Bernissartia* could hardly have eaten full-grown individuals. Mollusc-eating habits thus seem likely enough for *Bernissartia*, although this does not preclude the catching of other kinds of prey; while the posterior teeth had a crushing function, the anterior ones obviously formed a prehensile apparatus, as in other crocodilians. The shape of the lower jaw, known from the Brussels specimen (Pl. 122, figs. 27, 29), differs somewhat from that of other tribodont crocodilians. In *O. tetraspis*, and even more in *Allognathosuchus*, the mandible is strongly built, and in lateral view its dorsal edge is much undulated. In *Bernissartia* the jaw is more slender and the undulations are less marked. In these respects *Bernissartia* appears to have been less specialized than later tribodont crocodilians, but what functional implications that may have entailed is not quite clear. The bite of *Bernissartia* may have been less powerful than that of *Allognathosuchus*, for instance, but nevertheless it was certainly sufficient to allow the posterior crushing teeth to function adequately.

There does not seem to be any close phyletic relationships between the distinct groups of tribodont crocodilians. It is probable that crushing teeth were independently acquired in several groups of small crocodilians sharing a common diet of hard-shelled animals. The frequent occurrence of a tribodont dentition in early alligatorids is rather remarkable, but presumably indicates independent specialization rather than direct descent from *Bernissartia*.

Acknowledgements. We wish to thank Dr. Colin Patterson, of the British Museum (Natural History), who established that the teeth were not those of a fish, Dr. Alan Charig and Mr. C. A. Walker, also of the B.M.(N.H.), for the opportunity to see the specimen of '*Crocodilus saulii*', Dr. P. Sartenaer and Dr. P. Bultynck (Institut Royal des Sciences Naturelles de Belgique, Brussels), for permission to study the type specimen of *Bernissartia fagesii*, Dr. D. Baird (Princeton University) for the loan of *Brachychampsa* and *Allognathosuchus* teeth, Dr. J. P. Gasc (Laboratoire d'Anatomie Comparée, Muséum National d'Histoire Naturelle, Paris), for allowing the inspection of specimens of *Osteolaemus tetraspis*, and Professor M. Crusafont-Pairo (Sabadell) and Professor B. Krebs (Berlin) for information on crocodilian teeth from Galve.

REFERENCES

ABEL, O. 1928. *Allognathosuchus*, ein an die cheloniphage Nahrungsweise angepasster Krokodiltypus des nordamerikanischen Eozäns. *Paläont. Z.* **9**, 367–374, 1 fig.

ANTUNES, M. T. 1962. Presença de *Osteolaemus tetraspis* nas lagoas asfalticas de Sassa-Zau (Maiombe). *Estudos cientificos oferecidos em homenagem ao Prof. Doutor J. Carrington da Costa*, Lisbon, 67–76, 2 figs., 1 pl.

BERG, D. E. 1966. Die Krokodile, insbesondere *Asiatosuchus* und aff. *Sebecus*? aus dem Eozän von Messel bei Darmstadt/Hessen. *Abh. hess. Landesamt. Bodenforsch.* **52**, 1–105, 11 figs., 6 pls.

—— and CRUSAFONT-PAIRO, M. 1970. Note sur quelques Crocodiliens de l'Eocène prépyrénaïque. *Act. Geol. Hispanica*, **5**, 54–57, 1 fig.

BUFFETAUT, E. 1975. Sur l'anatomie et la position systématique de *Bernissartia fagesii* Dollo, L., 1883, Crocodilien du Wealdien de Bernissart, Belgique. *Bull. Inst. r. Sci. nat. Belg.* **51**, 2, 1–20, 4 figs., 4 pls.

CASE, E. C. 1925. Note on a new species of the Eocene crocodilian *Allognathosuchus*, *A. wartheni*. *Contr. Mus. Geol. Univ. Mich.* **2**, 93–97, 1 fig., 1 pl.

COTT, H. B. 1961. Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. *Trans. zool. Soc. Lond.* **29**, 211–356, 45 figs., 9 pls.

CRUSAFONT-PAIRO, M. and ADROVER, R. 1966. El primer Mamifero del Mesozoico español. *Publ. Catedra Paleontol. Univ. Barcelona*, **13**, 28–33, 1 fig.

DOLLO, L. 1883. Première note sur les Crocodiliens de Bernissart. *Bull. Mus. r. Hist. nat. Belg.* **2**, 309–338, 1 pl.

ERICKSON, B. R. 1972. *Albertochampsa langstoni*, gen. et sp. nov., a new alligator from the Cretaceous of Alberta. *Sci. Publ. Sci. Mus. Minn.* N.S. **2**, 1–13, 5 figs.

GILMORE, C. W. 1911. A new fossil alligator from the Hell Creek beds of Montana. *Proc. U.S. natn. Mus.* **41**, 297–302, 1 fig., 2 pls.

KÄLIN, J. 1941. Über die Altersvariationen von *Osteolaemus tetraspis* Cope und über '*Osteoblepharon osborni* K. P. Schmidt'. *Zool. Anz.* **134**, 295–299, 2 figs.

LANGSTON, W. 1965. Fossil crocodilians from Colombia and the Cenozoic history of the Crocodilia in South America. *Univ. Calif. Publs geol. Sci.* **52**, 1–157, 48 figs., 1 pl.

—— 1974. Nonmammalian Comanchean tetrapods. *Geosci. & Man*, **8**, 77–102, 10 figs., 4 pls.

LYDEKKER, R. 1888. *Catalogue of the fossil Reptilia and Amphibia in the British Museum* (*Nat. Hist.*), vol. I, British Museum, London.

OSBORNE WHITE, H. J. 1921. *A short account of the geology of the Isle of Wight*, Geological Survey of Great Britain, London.

OWEN, R. 1851. Monograph on the fossil Reptilia of the Cretaceous formations. *Palaeontogr. Soc.* (*Monogr.*), **5**, 11, 1–118, 37 pls.

—— 1884. *British fossil reptiles*, **2**, London.

SIMPSON, G. G. 1930. *Allognathosuchus mooki*, a new crocodile from the Puerco formation. *Am. Mus. Novit.* **445**, 1–16, 6 figs.

STEEL, R. 1973. *Crocodylia. Handbuch der Paläoherpetologie*, **16**, 1–116. G. Fischer, Stuttgart.

THURMOND, J. T. 1974. Lower vertebrate faunas of the Trinity division in north-central Texas. *Geosci. & Man*, **8**, 103–129, 15 figs., 1 pl.

WERMUTH, H. 1953. Systematik der rezenten Krokodile. *Mitt. zool. Mus. Berl.* **29**, 375–514, 66 figs.

WOODWARD, A. S. 1885. On the literature and nomenclature of British fossil Crocodilia. *Geol. Mag.* **2**, 496–510.

—— 1886. The history of fossil crocodiles. *Proc. Geol. Ass.* **9**, 288–344, 25 figs.

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Typescript received 9 May 1978
Revised typescript received 19 October 1978